

Uniqueness of Primate Forelimb Posture During Quadrupedal Locomotion

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ABSTRACT Among the characteristics that are thought to set primate quadrupedal locomotion apart from that of nonprimate mammals are a more protracted limb posture and larger limb angular excursion. However, kinematic aspects of primate or nonprimate quadrupedal locomotion have been documented in only a handful of species, and more widely for the hind than the forelimb. This study presents data on arm (humerus) and forelimb posture during walking for 102 species of mammals, including 53 nonhuman primates and 49 nonprimate mammals. The results demonstrate that primates uniformly display a more protracted arm and forelimb at hand touch-down of a step than nearly all other mammals. Although primates tend to end a step with a less retracted humerus, their total humeral or forelimb angular excursion exceeds that of other mammals. It is suggested that these features are components of functional adaptations to locomotion in an arboreal habitat, using clawless, grasping extremities. *Am J Phys Anthropol* 112:87–101, 2000. © 2000 Wiley-Liss, Inc.

The form of quadrupedalism displayed by primates differs from that of nonprimate mammals in a variety of ways (Vilensky, 1987, 1989; Larson, 1998). Among these differences are large limb angular excursions (Alexander and Maloiy, 1984), brought about in part by a more protracted position of the limb at touchdown (Reynolds, 1987). These generalizations regarding limb posture and excursion, however, are based mainly on observations for the hind limb, and for very limited samples of either primates (Reynolds, 1987; Demes et al., 1990) or nonprimates (McMahon, 1975, 1984). Although a more protracted limb posture and larger angular excursion have been assumed to also characterize the primate forelimb (e.g., Schmitt et al., 1994), relatively little comparative data exist in support of this supposition (for review, see Larson, 1998). To explore the generality of this claim, the present study was undertaken to

survey forelimb posture and excursion during quadrupedal walking across the primate order, as well as for a variety of nonprimate mammals.

METHODS

Forelimb positional data were derived from videotapes of captive animals taken at the following zoos and research centers: Brookfield Zoo, Chicago, IL; Bronx Zoo, New York, NY; Cleveland Zoo, Cleveland, OH; Pittsburgh Zoo, Pittsburgh, PA; San Diego Zoo; San Diego, CA; Duke Primate Center, Durham, NC; Primate Locomotion Laboratory, Stony Brook, NY; and Laboratoire

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d'Ecologie Générale, CNRS/Unité de Recherche 1183, Brunoy, France. Most of the videotapes were recorded by one of the authors (S.G.L.) with a hand-held Panasonic AG 195 camcorder equipped with an electronic shutter (1/500 sec) at 60 fields/sec. Additional video was recorded by P.L. using a tripod-mounted Sony HandyCam Super 8-mm camcorder, and by M.H. using a tripod-mounted Panasonic PV 900 camcorder. In most cases the subjects were 5 or more meters from the camera, minimizing parallax problems (Plagenhoef, 1979; Winter, 1990). Video analysis was performed on a Panasonic AG-6300 VCR, using frame-by-frame playback (30 frames/sec) to identify steps in which the subject was traveling in a relatively straight path, approximately perpendicular to the line of sight of the camera. Only walking gaits were analyzed of steps on substrates inclined no more than 20° to the horizontal.

Video images were imported into a 486 microcomputer with a PC-Vision+ video frame grabber board, and digitized for quantitative analysis with Java Video Analysis computer software from Jandel Scientific (Sausalito, CA). The orientation of the arm (shoulder to elbow) and the entire forelimb (shoulder to contact point) relative to the trunk (shoulder to hip) at hand touchdown and liftoff were digitized, as well as the inclination of the trunk relative to horizontal and the orientation of the substrate. The angles of the humerus and forelimb relative to a line perpendicular to the substrate passing through the shoulder joint at hand touchdown and lift-off were later computed trigonometrically. As no significant differences were found between steps on horizontal substrates compared to the slightly inclined or declined substrates (20° or less), all steps for a species were pooled and limb angles are described as being relative to a vertical line passing through the shoulder joint.

Given the nature of the data source, it was not possible to control for speed or substrate type, or to correct for any out-of-plane motion. In addition, it should be emphasized that none of the zoo subjects were shaved to help identify joint centers. While bony landmarks indicating joint positions

can in most cases be easily identified on larger animals, the fur of very small subjects tends to obscure such landmarks. These data, then, are at best approximations of limb posture kinematics. However, as an indication of the accuracy of these methods, arm angle data at hand touchdown and liftoff collected here for two primate species, *Chlorocebus aethiops* and *Saimiri sciureus*, were compared to information published by Vilensky and Gankiewicz (1990) and Vilensky et al. (1994)¹ acquired under more controlled laboratory conditions. In all cases, the published values fell within one standard deviation of our species means.

Video data were collected on 95 quadrupedal mammalian species. Data on an additional 7 species of nonprimate mammals were derived from the literature (see Table 1) to yield a total of 102 species, including 53 primates and 49 nonprimates. The nonprimate sample included 4 marsupials, 7 rodents, 23 carnivores, 13 ungulates, 1 hyrax, and 1 tupioid. Since the latter two were the sole representatives of their orders, for simplicity of comparisons, they were grouped with the rodents because of their similar body size and form. The primate sample included 10 lorisooids, 7 lemuroids, 14 ceboid species, 18 cercopithecooids, and 4 hominoids. All nonprimate species were within the size range of nonhuman primates (60 g–160 kg).

An effort was made to digitize at least 10 steps from every species, but this was not always possible.² Mean values for limb angles for each species were grouped into orders. Since limb excursion angles are potentially correlated to body size (McMahon, 1975, 1984), differences between mammalian orders were analyzed with ANCOVAs, using the General Linear Models Procedure of SAS (SAS Institute, Cary, NC, 1988), with the angle of interest being the dependent y-variable, and body size being the independent x-variable (Sokal and Rohlf, 1981). The procedure computed

¹In both cases, published values were estimated from graphs.

²The number of steps analyzed from the videotapes is included in Table 1.

TABLE 1. List of species studied

Species	Common name	Body size (kg) ¹	No. of steps analyzed
Primates²			
Cheirogaleids			
<i>Cheirogaleus major</i>	Greater dwarf lemur	0.40	31
<i>Cheirogaleus medius</i>	Fat-tailed dwarf lemur	0.28	22
<i>Microcebus murinus</i>	Gray mouse lemur	0.12	27
<i>Mirza coquereli</i>	Coquerel's dwarf lemur	0.31	18
Galagids			
<i>Galago senegalensis</i>	Senegal bushbaby	0.19	9
<i>Otolemur garnetti</i>	Small-eared greater bushbaby	0.76	66
Lorisids			
<i>Loris tardigradus</i>	Slender loris	0.19	31
<i>Nycticebus coucang</i>	Slow loris	0.65	21
<i>Nycticebus pygmaeus</i>	Pygmy slow loris	0.42	30
<i>Perodicticus potto</i>	Potto	1.10	23
Lemurids			
<i>Eulemur coronatus</i>	Crowned lemur	1.65	7
<i>Eulemur fulvus</i>	Brown lemur	2.21	39
<i>Eulemur macaco</i>	Black lemur	2.44	62
<i>Eulemur mongoz</i>	Mongoose lemur	1.62	26
<i>Hapalemur griseus</i>	Gentle lemur	0.94	40
<i>Lemur catta</i>	Ring-tailed lemur	2.21	28
<i>Varecia variegata</i>	Ruffed lemur	3.49	38
Cebids			
<i>Aotus trivirgatus</i>	Owl monkey	0.77	21
<i>Cebuella pygmaea</i>	Pygmy marmoset	0.12	3
<i>Cebus albifrons</i>	White-fronted capuchin	2.73	10
<i>Cebus apella</i>	Tufted capuchin	3.08	15
<i>Saguinus geoffroyi</i>	Geoffroy's tamarin	0.49	3
<i>Saguinus midas</i>	Golden-handed tamarin	0.54	5
<i>Saimiri sciureus</i>	Squirrel monkey	0.72	12
Atelids			
<i>Alouatta caraya</i>	Black howler monkey	5.37	3
<i>Alouatta seniculus</i>	Red howler monkey	5.95	26
<i>Ateles belzebuth</i>	Long-haired spider monkey	8.07	11
<i>Ateles paniscus</i>	Black spider monkey	8.77	14
<i>Callicebus moloch</i>	Dusky titi monkey	0.99	5
<i>Lagothrix lagothricha</i>	Woolly monkey	7.15	14
<i>Pithecia pithecia</i>	White-faced saki	1.76	15
Cercopithecines			
<i>Cercocebus galeritus</i>	Tana River mangabey	7.40	18
<i>Cercopithecus ascanius</i>	Red-tailed monkey	3.31	5
<i>Cercopithecus diana</i>	Diana monkey	4.55	19
<i>Cercopithecus lhoesti</i>	L'Hoest's monkey	4.71	2
<i>Cercopithecus mitis</i>	Blue monkey	6.09	26
<i>Cercopithecus neglectus</i>	De Brazza's monkey	5.74	1
<i>Chlorocebus aethiops</i>	Vervet monkey	3.62	27
<i>Erythrocebus patas</i>	Patas monkey	9.45	23
<i>Macaca fascicularis</i>	Long-tailed macaque	4.48	17
<i>Macaca mulatta</i>	Rhesus macaque	9.90	26
<i>Mandrillus sphinx</i>	Mandrill	22.25	29
<i>Miopithecus talapoin</i>	Talapoin monkey	1.25	13
<i>Papio anubis</i>	Olive baboon	19.20	20
Colobines			
<i>Colobus angolens</i>	Angolan colobus monkey	8.62	7
<i>Nasalis lavartus</i>	Proboscis monkey	20.40	7
<i>Pygathrix nemaeus</i>	Douc langur	9.72	9
<i>Trachypithecus cristata</i>	Silvered leaf monkey	6.18	4
<i>Trachypithecus francoisi</i>	Francois' leaf monkey	7.52	3
Pongids			
<i>Gorilla gorilla</i>	Lowland gorilla	121.00	21
<i>Pan paniscus</i>	Bonobo	38.20	4
<i>Pan troglodytes</i>	Chimpanzee	53.00	21
<i>Pongo pygmaeus</i>	Orangutan	57.00	18

(continued)

TABLE 1. Continued

Species	Common name	Body size (kg) ¹	No. of steps analyzed
Carnivores			
<i>Acinonyx jubatus</i>	Cheetah	53.50	10
<i>Ailurus fulgens</i>	Red panda	4.00	11
<i>Arctictis binturong</i>	Binturong	11.50	8
<i>Canis familiaris</i> ³	Domestic dog	11.25	
<i>Cryptoprocta ferox</i>	Fossa	9.50	6
<i>Eira barbara</i>	Grey-headed tayra	4.50	9
<i>Felis caracal</i>	Caracal	16.00	26
<i>Felis catus</i> ⁴	Domestic cat	3.50	
<i>Felis silvestris</i>	Wild cat	5.50	3
<i>Felis wiedii</i>	Margay	6.50	2
<i>Hyaena hyaena</i>	Striped hyaena	40.00	15
<i>Martes flavigula</i>	Yellow-throated marten	2.50	2
<i>Mephitis mephitis</i>	Striped skunk	1.75	1
<i>Mungos mungo</i>	Banded mongoose	1.60	11
<i>Mustela putorius</i> ⁵	European polecat	0.90	
<i>Nasua nasua</i>	Brown coati	4.00	5
<i>Neofelis nebulosa</i>	Clouded leopard	19.50	3
<i>Panthera onca</i>	Jaguar	85.00	12
<i>Panthera pardus</i>	Leopard	60.00	11
<i>Procyon lotor</i>	Raccoon	6.50	2
<i>Suricata suricatta</i>	Meerkat	0.79	10
<i>Tremarctos ornatus</i>	Spectacled bear	100.00	24
<i>Vulpes corsac</i>	Corsac fox	5.50	7
Marsupials			
<i>Caluromys philander</i>	Woolly opossum	0.30	10
<i>Dendrolagus matschiei</i>	Tree kangaroo	7.20	9
<i>Didelphis virginiana</i> ⁶	Virginia opossum	2.31	
<i>Phascolarctos cinereus</i>	Koala	9.30	10
Rodents			
<i>Dasyprocta aguti</i>	Orange-rumped agouti	2.65	15
<i>Dinomys branickii</i>	Pacarana	12.50	2
<i>Dolichotis patagonum</i>	Patagonian cavy	12.50	6
<i>Heterohyrax brucei</i> ^{5,7}	Gray hyrax	1.20	
<i>Hydrochaeris hydrochaeris</i>	Capybara	50.50	1
<i>Mesocricetus auratus</i> ⁵	Golden hamster	0.10	
<i>Myoprocta acouchy</i>	Acouchy	0.95	3
<i>Rattus norvegicus</i> ⁵	Brown rat	0.50	
<i>Tupaia glis</i> ⁷	Tree shrew	0.17	3
Ungulates			
<i>Capricornis crispus</i>	Japanese serow	75.00	5
<i>Damaliscus dorcas</i>	Blesbok	91.50	6
<i>Gazella dama</i>	Mhorr's gazelle	57.50	7
<i>Gazella dorcas</i>	Dorcas gazelle	17.50	9
<i>Gazella soemmerringi</i>	Soemmerring's gazelle	42.00	1
<i>Madoqua guentheri</i>	Guenther's dik dik	4.60	5
<i>Muntiacus muntjac</i>	Muntjac	16.00	2
<i>Neotragus moschatus</i>	Suni	6.50	5
<i>Odocoileus virginianus</i>	Deer	150.00	4
<i>Ovis vignei</i>	Transcaspian urial	50.00	10
<i>Rangifer tarandus</i>	Reindeer	95.50	4
<i>Saiga tatarica</i>	Saiga antelope	47.00	10
<i>Sylvicapra grimmia</i>	Gray duiker	18.50	2

¹ Mean body sizes for species taken from the literature (average of male and female if reported separately). Sources: Macdonald (1984a,b); Nowak (1991); Smith and Jungers (1997).

² Taxonomy after Fleagle (1999).

³ Data from Nomura et al. (1966) and Tokuriki (1973).

⁴ Data from Miller and Van der Meché (1975) and English (1978a,b).

⁵ Data from Jenkins (1971).

⁶ Data from Jenkins and Weijs (1979).

⁷ Hyraxes and tree shrews are not rodents but members of the orders Hyracoidea and Scandentia, respectively. However, to simplify comparisons, they were grouped with the rodents because of their similar size and body form.

an adjusted mean (least squares mean) for each order, in which the effect of body size has been accounted for. In addition, the standard errors of the adjusted means,

and pairwise comparisons of statistical differences between means, were calculated. A similar procedure was performed on primate species grouped into families

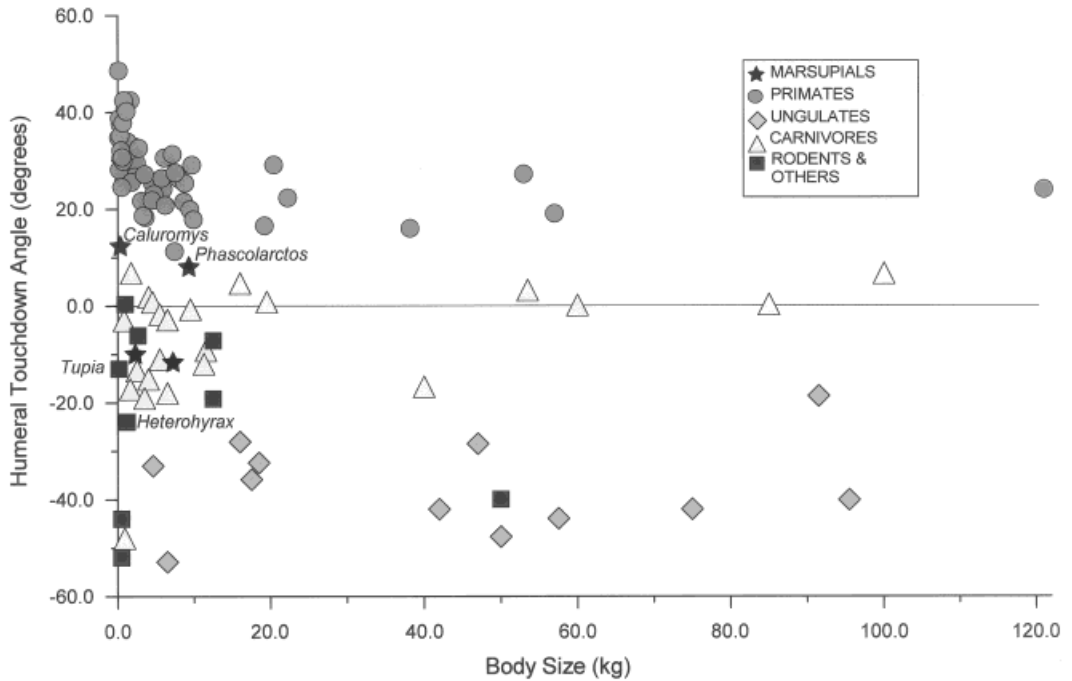


Fig. 1. Mean humeral touchdown angle plotted against mean body size (see Table 1) for each species. Angles are described relative to a vertical line passing through the shoulder to the substrate. Positive values denote a humerus positioned in front of the vertical; negative values reflect a position behind the vertical. Primates are represented by circles, marsupials by stars, carnivores by triangles, rodents (including the hyrax and tree shrew) by squares, and ungulates by

diamonds. Primates display larger humeral protraction angles than almost any other mammal. The notable exceptions are the woolly opossum, *Caluromys philander*, which is an arboreal, small-bodied species showing other convergences with primates in hand and foot proportions (Lemelin, 1996, 1999), and the koala, *Phascolarctos cinereus*, which also occupies an arboreal habitat.

or subfamilies to explore for differences across the order.

RESULTS

Figure 1 shows the angle of the humerus at touchdown relative to body size across the sample. The angles are expressed relative to a vertical line through the shoulder: positive values reflect a humerus that is ahead of vertical, and negative numbers reflect a humerus that is positioned behind vertical. It is clear that at any body size, nonhuman primates have a more protracted humerus than any nonprimate mammal, with the interesting exception, *Caluromys philander*, being an arboreal marsupial. The koala (*Phascolarctos cinereus*), another arboreal marsupial, also approaches the primate range.

For ease of comparison, Figure 2 presents a graph of just the group means for protrac-

tion angle at touchdown, retraction angle at liftoff, and total angular excursion of the humerus and of the entire forelimb for each of the mammalian groups. The positive touchdown angle of the humerus of primates stands in marked contrast and is significantly different from those of the other mammalian groups (Table 2). Primate humeri are also less retracted at liftoff than those of other mammalian groups, and again this difference is statistically significant. Even though primates do not retract their humeri as far as other mammalian groups during a step, the total excursion of the arm is still significantly greater than that of all other mammalian groups except the marsupials.

The excursion angles of the forelimb reflect how these differences in humeral excursion affect the motion of the entire limb. Although all mammals display a protracted

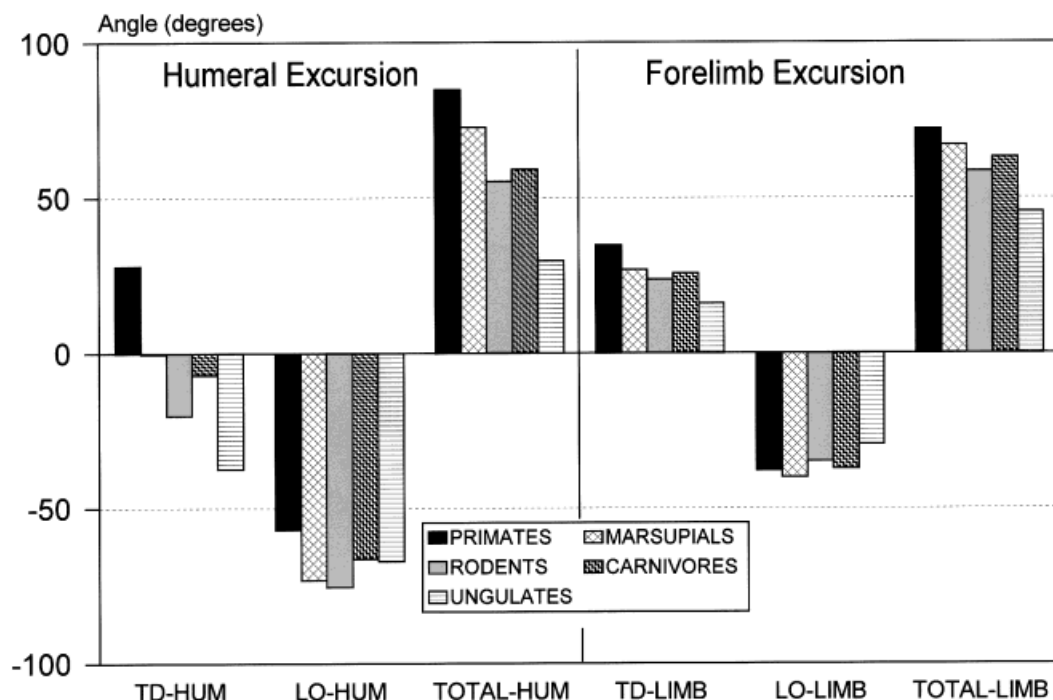


Fig. 2. Raw mean humeral and forelimb excursion angles for all mammalian groups sampled. Angles are expressed relative to a vertical line passing through the shoulder. Total humeral excursion angle (TOTAL-HUM) equals humeral touchdown angle (TD-HUM)

plus the absolute value of humeral liftoff angle (LO-HUM). Similarly, total forelimb excursion angle (TOTAL-LIMB) equals forelimb touchdown angle (TD-LIMB) plus the absolute value of forelimb liftoff angle (LO-LIMB). See text for further discussion.

forelimb at touchdown since the forefoot must land ahead of the shoulder to prevent the animal from falling forward, the degree of forelimb protraction at touchdown is again significantly greater in primates. There are no significant differences between any of the groups in the degree of forelimb retraction at liftoff; however, the total angular excursion of the forelimb is still larger in primates compared to the other mammalian groups (statistically different for all except the marsupials).

Figure 3 displays a schematic representation of these differences in limb posture across mammals. The cartoons are drawn as if the animals are all the same size and share equal total limb lengths (humerus + forearm length). However, the relative proportions of the proximal to distal limb segment lengths have been adjusted to more realistically portray the limbs of cursorily adapted species (carnivores and ungulates) and noncursorial species (marsupials and

rodents). In each case, the small dark triangle represents humeral excursion, and the lighter triangle is total forelimb excursion. The distal limb segment was simply drawn to connect the distal end of the humerus to the line representing the forelimb angle, and therefore, elbow angles should not be taken as necessarily accurate. The position of the liftoff foot above the substrate is likely due to unaccounted-for scapular motion, which unfortunately could not be documented in this study. As illustrated in Figure 3, not only do primates utilize larger humeral and forelimb excursion angles, but their limb excursion is more nearly symmetric around a vertical line from the shoulder to the substrate.

Having shown that primates as a group differ from other mammalian groups, it is also important to consider whether there is variation in these postural characteristics within primates. Figure 4 displays mean humeral and forelimb angles for the pri-

TABLE 2. Raw and least square means for sample species grouped into orders

TD-HUM	MEAN	LSMEAN	Std err LSMEAN	Probability level for H_0 : LSMEAN(i) = LSMEAN(j)				
					Marsupials	Rodents	Ungulates	Primates
Primate	28.07	28.06	1.44					
Carnivores	-7.08	-7.08	2.12	Carnivores	0.2281	0.0039	0.0001	0.0001
Marsupials	-0.34	-0.37	5.10	Marsupials		0.0026	0.0001	0.0001
Rodents	-20.05	-20.06	3.84	Rodents			0.0010	0.0001
Ungulates	-37.30	-37.23	3.15	Ungulates				0.0001
LO-HUM	MEAN	LSMEAN	Std err LSMEAN	Probability level for H_0 : LSMEAN(i) = LSMEAN(j)				
					Marsupials	Rodents	Ungulates	Primates
Primates	-56.82	-55.08	1.67					
Carnivores	-66.25	-66.78	2.45	Carnivores	0.5743	0.1577	0.0783	0.0002
Marsupials	-73.13	-70.39	5.91	Marsupials		0.6232	0.5606	0.0138
Rodents	-75.30	-74.03	4.45	Rodents			0.9318	0.0001
Ungulates	-67.04	-74.53	3.65	Ungulates				0.0001
TOTAL-HUM	MEAN	LSMEAN	Std err LSMEAN	Probability level for H_0 : LSMEAN(i) = LSMEAN(j)				
					Marsupials	Rodents	Ungulates	Primates
Primates	84.89	83.14	2.00					
Carnivores	59.17	59.71	2.94	Carnivores	0.1822	0.3494	0.0001	0.0001
Marsupials	72.78	70.02	7.08	Marsupials		0.0725	0.0002	0.0762
Rodents	55.25	53.97	5.33	Rodents			0.0191	0.0001
Ungulates	29.73	37.30	4.37	Ungulates				0.0001
TD-HUM	MEAN	LSMEAN	Std err LSMEAN	Probability level for H_0 : LSMEAN(i) = LSMEAN(j)				
					Marsupials	Rodents	Ungulates	Primates
Primates	34.73	33.97	0.76					
Carnivores	25.74	25.91	1.12	Carnivores	0.4631	0.3582	0.0003	0.0001
Marsupials	26.87	23.51	3.04	Marsupials		0.9975	0.1527	0.0012
Rodents	23.69	23.50	2.35	Rodents			0.0825	0.0001
Ungulates	16.03	18.46	1.62	Ungulates				0.0001
LO-HUM	MEAN	LSMEAN	Std err LSMEAN	Probability level for H_0 : LSMEAN(i) = LSMEAN(j)				
					Marsupials	Rodents	Ungulates	Primates
Primates	-37.79	-37.08	0.95					
Carnivores	-37.33	-37.53	1.39	Carnivores	0.8256	0.3616	0.0379	0.7916
Marsupials	-40.03	-38.42	3.77	Marsupials		0.4210	0.1708	0.7305
Rodents	-34.81	-34.57	2.91	Rodents			0.5480	0.4136
Ungulates	-29.44	-32.42	2.01	Ungulates				0.0471
TOTAL-HUM	MEAN	LSMEAN	Std err LSMEAN	Probability level for H_0 : LSMEAN(i) = LSMEAN(j)				
					Marsupials	Rodents	Ungulates	Primates
Primates	72.09	70.96	1.37					
Carnivores	63.08	63.44	2.00	Carnivores	0.7969	0.2520	0.0005	0.0027
Marsupials	66.90	61.94	5.44	Marsupials		0.5744	0.0802	0.1095
Rodents	58.50	58.07	4.20	Rodents			0.1633	0.0044
Ungulates	45.47	50.87	2.90	Ungulates				0.0001

mate sample sorted by families (with the two subfamilies of cercopithecoids also separated). The families are arranged from smallest to largest average body size,³ suggesting some influence of overall size on humeral excursion, with a pattern of decreasing

degree of protraction and retraction of the humerus at touchdown and liftoff leading to smaller total humeral excursion as average body size increases. However, it is clear that in all primate families, the humerus touches down in a protracted position (see Table 3). Despite these differences in humeral excursion angles, forelimb excursion angles appear fairly uniform across primates, especially limb angle at touchdown. While there is some indication of decreasing

³Average body size for the lemurids actually exceeds that of the cebids sampled here, but they were put in reverse order in Figure 4 so that the lemurids could be more directly compared with the other prosimian families, and the cebids could be compared to the atelids.

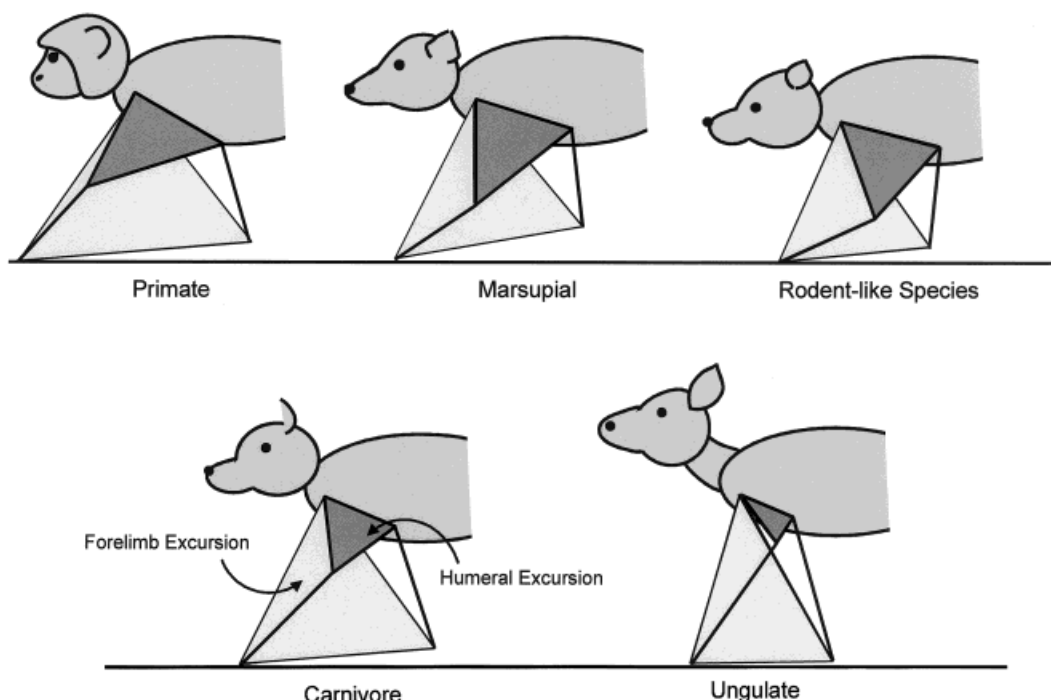


Fig. 3. Schematic representations of limb postures in different mammalian groups constructed from mean humeral and forelimb excursion angles. In all cartoons, body size and total forelimb length (proximal + distal segments) are equal. However, the relative proportions of the proximal and distal segments have been adjusted to better reflect typical limb proportions in different

mammalian groups. Larger, lightly shaded triangles represent total forelimb excursion, i.e., the difference between forelimb touchdown angle and forelimb liftoff angle. Smaller, darkly shaded triangles similarly represent total humeral excursion. See text for further discussion.

limb retraction angle and decreasing total excursion with increasing body size, the differences are small, and most are not statistically significant.

DISCUSSION

The video data analyzed here were collected under less than ideal conditions. Nonetheless, the results suggest that the differences between primates and nonprimate mammals are so large that even these inexact techniques reveal meaningful information. All quadrupedal primates begin a walking step with a protracted humerus and retract the limb through a large angular excursion as the step proceeds. This contrasts sharply with the either vertical or retracted position of the humerus at touchdown and smaller excursion angles of most other quadrupedal mammals. While these statements are broadly true across primates, there is some variability within the

order, and these differences certainly merit further study. However, analysis of more subtle kinematic differences requires greater uniformity in variables such as substrate type and speed, and are therefore probably best pursued in a more controlled laboratory setting.

The protracted position of the humerus in primates results in a more obtuse glenohumeral joint angle, and thus a more vertically aligned scapula and humerus. This is in contrast to a more acute glenohumeral angle and more crouched posture of most other noncursorial mammals. Scapular and humeral alignment increases the effective length of the limb and augments the already relatively long limb bone segments (femur, tibia, humerus, and ulna) of primates (Alexander et al., 1979). Since limb length and limb angular excursion are directly related to stride length, one might propose that the combination of a long forelimb with large

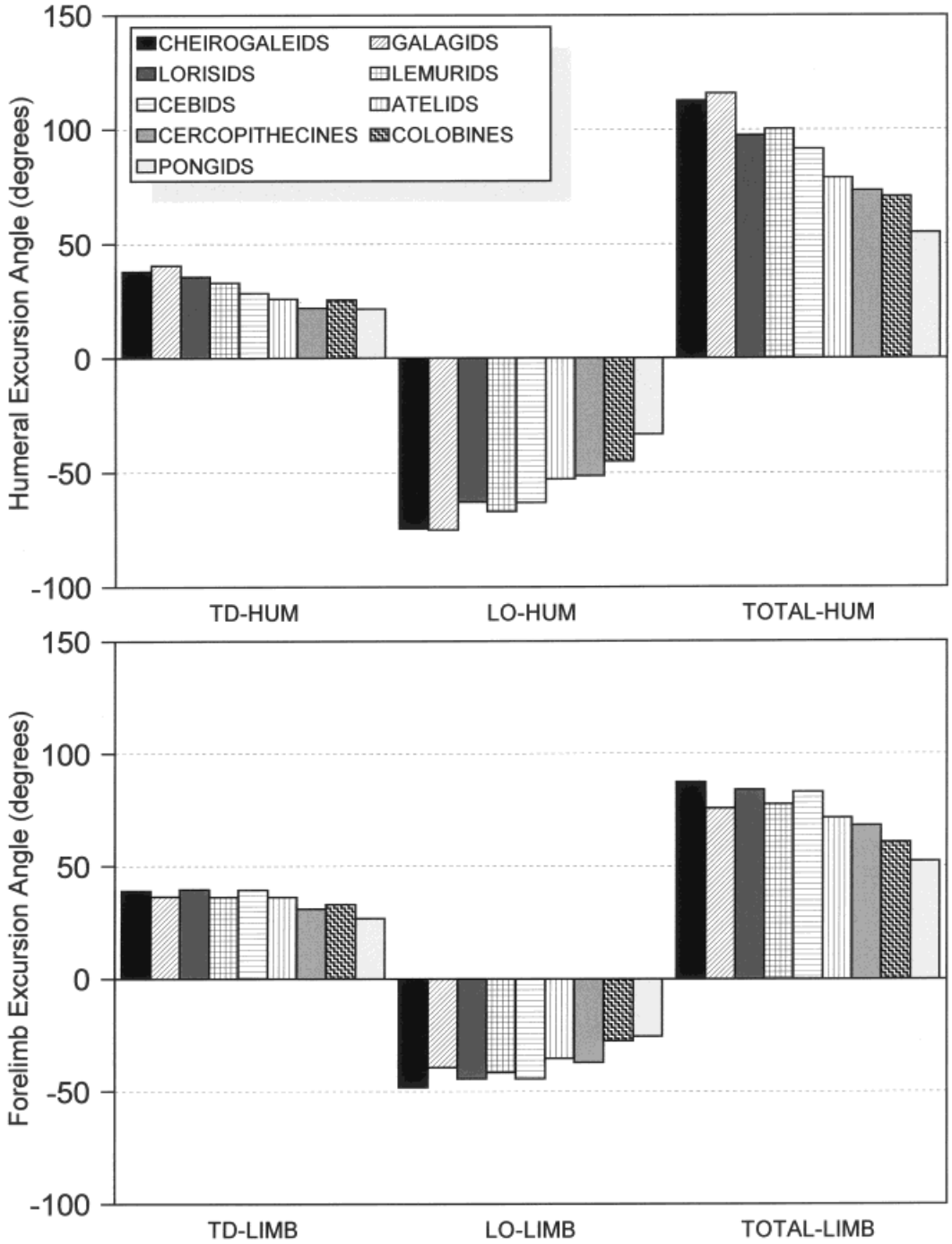


Fig. 4. Raw mean humeral and forelimb excursion angles for primates sorted into families, with the cercopithecoids separated into subfamilies Cercopithecinae and Colobinae (taxonomic sorting taken from Fleagle, 1999). Groups are arranged from smallest to largest average body size with the exception of the lemurs and cebids, which are switched in order to make more direct comparisons with other members of their superfamilies. See text for discussion.

angular excursion is for the purpose of increasing relative stride length, which has indeed been documented for nonhuman primates (Vilensky, 1980; Alexander and Maloiy, 1984; Reynolds, 1987). However, what advantage long stride length offers primates has remained unclear.

Stride length times the rate of stride equals speed, and therefore, animals presumably may change either or both to achieve different speeds. Since primates use relatively low stride frequencies (Alexander et al., 1979; Reynolds, 1987), long stride length may be a compensation to maintain speed. Indeed, Demes et al. (1990) argued that at least in lorises, long stride length is a more effective way of achieving higher walking speeds in an arboreal habitat precisely because it does not entail high stride frequency. Fast, high-frequency gaits produce steeply rising, relatively high peak forces that could cause significant branch sway, which is both dangerous and energy-costly. In addition, lorises search for prey and avoid predators by being cryptic; thus, long, low-frequency strides that minimize branch swaying motions also avoid alerting either predator or prey.

However, most primates are not cryptic, and while there is continuing debate about whether the locomotor mode of the ancestral euprimate emphasized "grasp-leaping" (e.g., Martin, 1972; Szalay and Delson, 1979; Szalay and Dagosto, 1980; Dagosto, 1988; Gebo, 1989), vertical clinging and leaping (Napier and Walker, 1967), or arboreal, quadrupedal walking and running (e.g., Godinot and Jouffroy, 1984; Ford, 1988), there is little that suggests a form of cautious quadrupedalism as in lorises. In this context, what advantage do forelimb protraction, large angular excursion, and limb elongation offer besides increased stride length?

Limb elongation, at least, is seen in other mammals such as many carnivores and ungulates. The elongation observed in these forms, usually grouped together as cursors, has been brought about by lengthening the distal elements of the limb, including the fingers (Alexander et al., 1979). Distal elongation is generally viewed as a means of reducing the inertial properties of the limb by concentrating mass proximally, thereby

making it easier to swing the limb forward and increasing running efficiency (Smith and Savage, 1956; Hildebrand, 1988). However, in so doing, these animals have sacrificed any ability to grasp with their hands or feet. Alternatively, those mammalian species that have retained more grasping extremities tend to have relatively shorter limbs.

By lengthening the proximal and intermediate limb segments, primates have evolved the unique combination of relatively long limbs with grasping extremities. According to most proposals that have been offered to explain the origins of primates, the evolution of clawless grasping extremities is related to travel and foraging in a small-branch arboreal setting (Cartmill, 1972, 1974, 1992; Garber, 1980; Rasmussen, 1990; Sussman, 1991; Hamrick, 1998; for a contrary view, see Soligo and Müller, 1999). Is there any reason why elongated limbs and a more protracted forelimb posture should also be associated with this environment? We suggest that *reaching out* with clawless, grasping hands in a small-branch setting forms the foundation for the distinctive primate forelimb posture during walking. It is interesting to note in this context that one nonprimate species that displays a degree of humeral protraction within the primate range, *Caluromys philander*, also uses grasping extremities to travel and forage in a small-branch setting, and shows other convergences in hand and foot proportions to cheirogaleid primates (Lemelin, 1996, 1999). Similarly, the species displaying the next closest forelimb protraction angle to that of primates is the koala (*Phascolarctos cinereus*), also an arboreal, climbing-adapted marsupial.

To travel or forage in an arboreal small-branch habitat using clawless, grasping hands, an animal must be able to reach out precisely to gain a secure grip on a particular branch or object. This is especially true of the climbing and scrambling forms of locomotion usually associated with the small-branch milieu. Nonstereotypical forelimb motion demands versatility in the neural control of limb movement, and as Georgopoulos and Grillner (1989) have shown, this entails a greater degree of supraspinal con-

trol⁴ of forelimb movements. They also report that the corticospinal input involved in correct positioning of the forelimbs during locomotion is the same as that involved in forelimb manipulatory movements. Georgopolulos and Grillner (1989) propose that the ability to use the forelimb for manipulation evolved from the ability to accurately position the limb during locomotion.

It follows that as supraspinal control of precise locomotor forelimb positioning developed, so did fine control of forelimb movement for foraging and manipulation. However, use of the forelimb for foraging, manipulation, and nonstereotypical locomotor motions also depends on enhanced mobility at the forelimb joints to increase the range of motion of the limb. Larson (1998) pointed out that increasing the mobility of joints generally can only be accomplished at the expense of stability, and cannot develop if the forelimbs are subjected to large disruptive locomotor forces. She suggested that many of the distinctive characteristics of primate quadrupedal locomotion can be related to mechanisms that primates utilize to attenuate the disruptive forces to which the forelimbs are subjected. Among these mechanisms are alteration of muscle recruitment patterns (Larson and Stern, 1989; Vilensky and Larson, 1989; Larson, 1998), greater reliance on the hind limbs than the forelimbs for both support and propulsion (Kimura et al., 1979; Kimura, 1985; Reynolds, 1985; Demes et al., 1992, 1994), and use of a more compliant gait (Schmitt, 1995, 1998, 1999).

A compliant gait is characterized by substantial limb yield (joint flexion during stance phase) during a step, longer step length, and longer contact time compared to a stiffer walk. The mechanics of compliant gait have been described in detail elsewhere (Alexander, 1977, 1992; Taylor, 1985; McMahon, 1985; McMahon et al., 1987; Blickhan, 1989; Farley et al., 1993; Schmitt, 1995, 1998, 1999), and will only be briefly summarized here. Long step length and long contact time reduce peak stresses act-

ing on the limb by increasing the time over which they develop. While it has often been postulated that primates crouch when walking on branches to lower their center of mass to better maintain balance (e.g., Napier, 1967; Grand, 1968a,b, 1984; Fleagle, 1978; Morbeck, 1979; Cartmill, 1985), Schmitt (1995, 1998, 1999) has documented that this crouch is brought about in a compliant manner by increasing elbow yield during support phase, which also increases contact time. In addition, elbow yield helps reduce vertical oscillations of the body's center of mass, giving it a lower, flatter trajectory (Schmitt, 1995, 1998). We suggest that initial limb protraction also lowers the body's center of mass at the beginning of a step. More importantly, beginning a step with the forelimb in a protracted position and then having it pass through a large angular excursion has the effect of further increasing step length and contact time. Thus the combination of elbow yield associated with a compliant gait, and initial limb protraction, work together to produce a crouching posture that is critical for maintaining balance and stability on a branch, as well as reducing the tendency to cause branch sway. They thereby augment the increased stabilization brought about directly by increased contact time (Cartmill, 1985; Demes et al., 1990; Schmitt, 1995, 1998, 1999). Finally, it should be noted that some kinetic advantage may derive from initial limb protraction alone. McMahon et al. (1987) have demonstrated that by changing the "angle of attack" of a limb, a protracted limb position at touchdown reduces vertical landing speed and vertical stiffness of the body, which attenuates some of the forces associated with impact.

Thus the unique characteristics of primate forelimb posture during walking observed here can be seen as integral components of several mechanisms that help reduce disruptive locomotor forces on forelimb joints, as well as increase security on small branches. However, current consensus suggests that the earliest primates were very small, perhaps mouse size (Martin, 1972; Cartmill, 1974; Dagosto and Teranova, 1992; Rose, 1995; for a contrary view, see Soligo and Müller, 1999), and it is

⁴Uncomplicated locomotion on an even surface is believed to be controlled largely by the spinal cord in most animals.

unclear just how disruptive locomotor forces might be on the forelimb joints of such small animals. Therefore, the development of such things as a compliant gait may have not occurred until later in primate evolution, when larger species began to appear. As larger species evolved, however, adoption of these stabilizing and force reducing mechanisms would have been facilitated by preexisting forelimb elongation and protraction that had already evolved as functional adaptations to reaching out and securing grips in the discontinuous small-branch habitat.

In order to determine the validity of these proposals, it would be useful to know when a more protracted humeral posture and larger angular excursion first appeared in the evolution of primates. However, answering this question depends on being able to identify morphological correlates of these postural features. To this end, an investigation is currently underway (by S.G.L.) to identify traits of the scapula and proximal humerus distinguishing primates from non-primates that could be indicative of use of a more protracted humerus in early euprimates. Documentation of the appearance and distribution of such features in euprimate fossils will hopefully help us to better understand the early evolution and radiation of primates.

CONCLUSIONS

Primates are distinguished from most other mammals in displaying a more protracted forelimb posture and greater forelimb angular excursion during quadrupedal walking. We propose that these unique characteristics can be related to several interconnected selective factors that were involved in the successful occupation and radiation of primates in the arboreal small-branch niche.

In order to effectively travel and forage in a discontinuous, complex small-branch environment, early primates needed to be able to reach out and achieve a secure grip on a branch or a food object. This selected not only for clawless grasping extremities, but also for greater cortical control of forelimb movements. Limb elongation might also been advantageous in this context. As cortical control of the forelimb for locomotion

increased, so did forelimb manipulatory abilities improve, thus enhancing manual foraging. The increasing versatility in forelimb use would be augmented by greater mobility in forelimb joints to increase the range of motion. Greater joint mobility, in turn, would select for mechanisms that reduced the disruptive forces experienced by forelimb joints during locomotion, especially as species with larger body sizes evolved. These mechanisms could take advantage of the somewhat increased limb length and forward range of motion of the forelimb associated with reaching out for a secure grip, to begin a step with the limb in a more protracted position, and thereby increasing limb excursion as well as augmenting step length and contact time. These changes in gait would have the added advantages of increasing stability on small branches and reducing dangerous and energy-costly branch sway. Further increases in the degree of forelimb protraction and limb elongation associated with these gait changes might in turn improve the ability to reach out with the forelimb to move and forage in the small-branch habitat.

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